

## Behaviour and Host Relationships of *Dolichomutilla sycorax* (Smith) (Hymenoptera: Mutillidae, Sphecidae)

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**Abstract.**—Detailed biological information for species of Mutillidae is generally lacking. The following aspects of the biology of *Dolichomutilla sycorax* (Smith), based on laboratory observations of 10 specimens (9♀, 1♂) reared from a single nest of *Sceliphron spirifex* (Linnaeus) (Sphecidae), are described in detail and discussed: emergence from host nest, activity patterns, mating and grooming. The recorded host relations for *D. sycorax* are also discussed.

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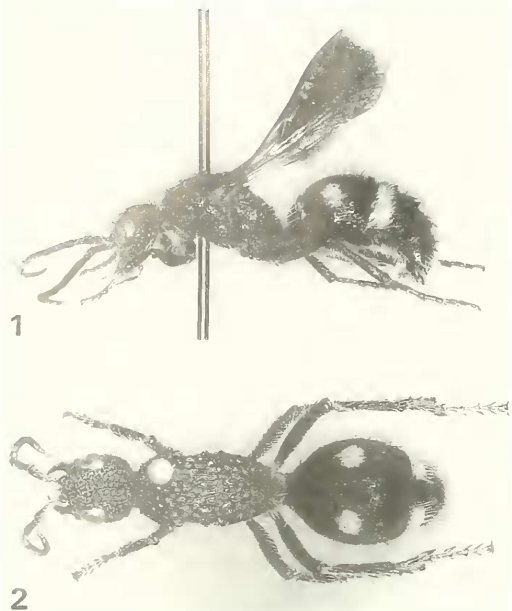
Successful mating by mutillid wasps generally requires only a short time (Brothers 1972), and very few observations have been recorded. These are important in providing information on sex associations. Grooming in mutillids has recently been described for the first time (Bayliss and Brothers 1996), and only in the last few years has it been used in systematic studies of the Hymenoptera (Basibuyuk and Quicke 1999). This paper provides the first descriptions of mating and grooming behaviour in *Dolichomutilla sycorax* (Smith) and surveys the data on its host relationships, as well as providing some other incidental information on the behaviour of this species.

*Dolichomutilla sycorax* is broadly distributed throughout eastern Africa, from Kenya to South Africa where it is the most common species of the genus. Its taxonomic status as a valid species distinct from *Dolichomutilla guineensis* (Fabricius) has recently been clarified by Nonveiller (1996). Specimens are approximately 9–22 mm long, with the head and metasoma black and the mesosoma deep marooned. The apterous females have a pair of white spots on the second metasomal tergum and an interrupted broad white band

on the third tergum; the macropterous males are almost identical in coloration, unlike for most Mutillidae, and have conspicuously banded wings (Figs. 1–2). Although Gerstaecker (1857, 1862) first described the male (misidentified as that of *D. guineensis*), presumably based on the similarity of the sexes, Péringuey (1898) was the first to associate the sexes directly, having reared both simultaneously from the mud nests of *Pelopaenus* [= *Sceliphron*] *spirifex* (Linnaeus) (Hymenoptera, Sphecidae).

### MATERIALS AND METHODS

Laboratory observations were made during April to December 1996 at the University of Natal, Pietermaritzburg. Live adults of *D. sycorax* were reared from a mud nest of *S. spirifex* collected at the Greater St Lucia Wetland Park, Ozabeni Section, Lower Mkuze, KwaZulu-Natal, South Africa (27°39'S, 32°26'E) on 6–9 April 1996 by R.M. Miller and J. Kotze. They emerged over a period of about 10 days (starting on 19 May 1996) and were kept isolated in petri dishes (diameter 90 mm, height 20 mm) after emergence. The bases of the dishes were lined with paper towelling to provide a rough substrate.



Figs. 1–2. *Dolichomutilla sycorax*. 1, ♂, lateral view (body length 10 mm). 2, ♀, dorsal view (body length 16 mm).

Mating was observed by placing two adults of opposite sex in the same petri dish; their behaviour was recorded using a Sony 8mm video camera and low-intensity cool fibre-optic illumination. The specimens were observed for at least 20 minutes, and if no interaction (including stridulation or rubbing of antennae) occurred between them during that time, they were separated for several hours before placing them together again.

A Wild M5 stereo microscope, using white light from a desk lamp, was used for observations of grooming at irregular intervals during the day and at night. Such behaviour was noted whenever seen, and detailed observations were carried out after sprinkling the body with flour. Observations (a total of at least 60) involved nine males and one female of *D. sycorax* that emerged from the mud nest and the full repertoire of cleaning activities was seen 12 times in seven different individuals (6♀, 1♂). The terminology

used in describing the grooming behaviour is from Basibuyuk and Quicke (1999).

After sufficient observations had been made, the specimens were released into a glass terrarium (288 × 217 × 225 mm, internal measurements) with the floor covered by fine sand to a depth of 25 mm and with several flattish stones to provide hiding places. Food (a solution of 10% honey dissolved in water) and water were provided in small glass tubes plugged with cotton wool. Most specimens lived for 3–10 months, the male surviving for the shortest period (8 weeks).

## RESULTS AND DISCUSSION

### Specimens Emerging from Mud Nest of Host

The mud nest comprised 15 more or less parallel cells separated by thick walls and with the outer walls thickened and roughened by the addition of extra mud. Within 16 days after the first recorded emergence, one male (12 mm long) and nine females (12–15 mm long) of *D. sycorax*, one specimen of *Stilbum cyanurum* (Förster) (Chrysididae) and two specimens of *Sceliphron spirifex* (one of each sex) had emerged. In addition, there were two cells containing host cocoons which produced hundreds of specimens of a species of *Melittobia* (Eulophidae). The rate of parasitism was thus 87%.

### Activity Patterns of *D. sycorax*

**Emergence.**—It took approximately 10 minutes for each individual, using the mandibles, to chew its way out of the cell. The antennae, followed by the head, first emerged through the newly chewed exit hole, and the surroundings were scanned. Since the forepart of the body is often slightly narrower than the posterior part, the metasoma was often unable to pass through the hole. The process of chewing would then be resumed until the hole was large enough for the entire body to pass through. After emergence, several minutes

were spent inspecting the nest, although no attempt was made to enter a previously vacated cell ( $n = 3$ ).

*Daily activity.*—Because of the artificial conditions of the terrarium, it is impossible to assume much about daily cycles. A female was placed together with the others in the terrarium only after the male had mated or interacted with her. The only male was kept in the terrarium with the mated females and his activity, as with the females, was monitored. At night all females huddled together under the same flat stone, even though there were several others of similar shape. The male was solitary, never resting with the females. The male died after 55 days, while the females lived for approximately 6 months. One female lived for almost 11 months.

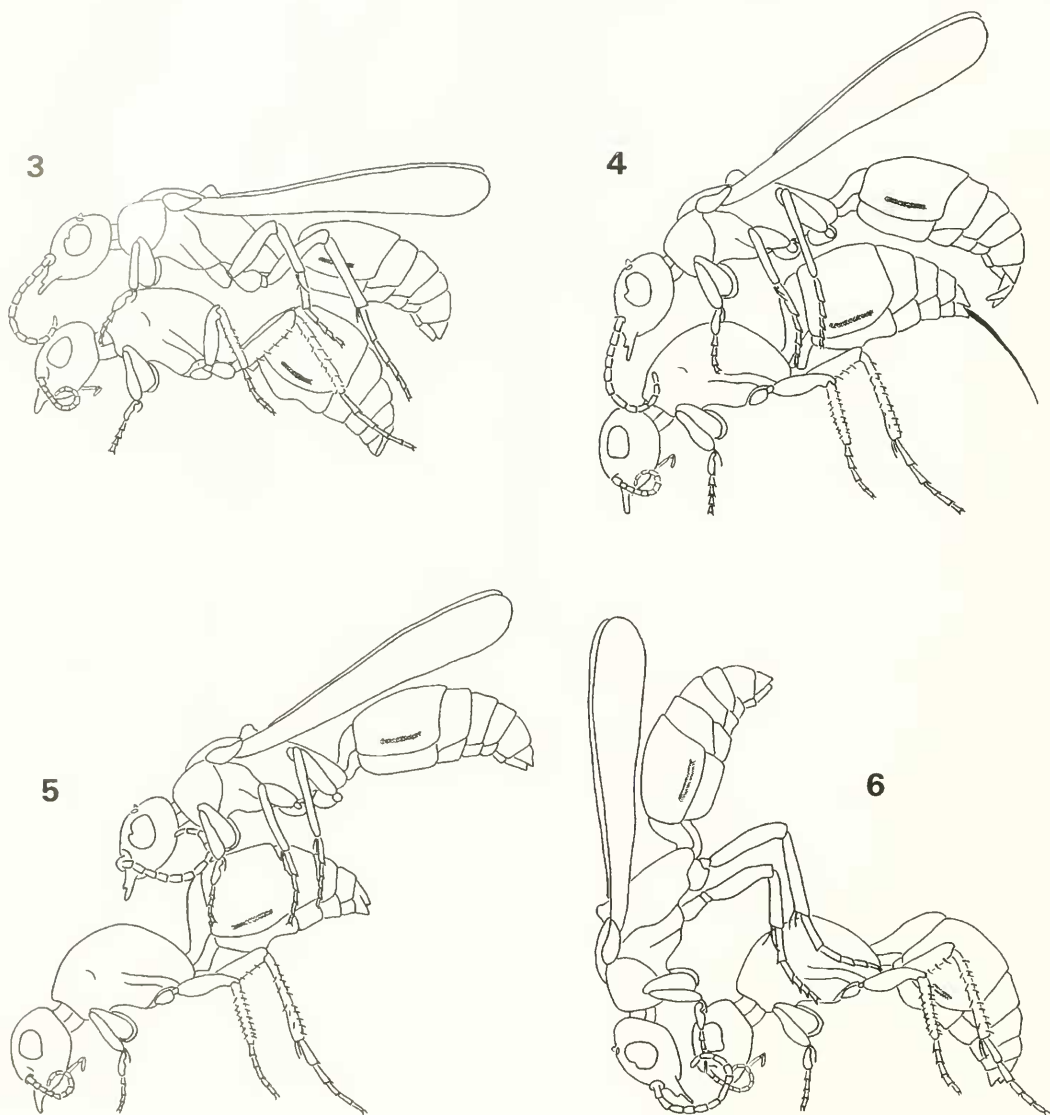
### Mating

Immediately after a male and a female were placed together in a petri dish, after having been kept in separate vials ( $n = 5$ ), they initially tried to escape by running. Whenever the two individuals came into contact head-on, both instantly showed avoidance or escape reactions by moving away in different directions. This is similar to Ferguson's (1962) observations on *Sphaerophthalma* (*Photopsis*) *blakeii* (Fox) but contrary to Brothers' (1972) observations on *Pseudomethoca frigida* (Smith) and Bayliss and Brothers' (1996) observations on *Tricholabiodes* spp. where neither member showed avoidance reactions. As soon as the male contacted the female, except when head-on, his antennae began to vibrate rapidly and continuously over her body. Within seconds he attempted to mount her. The female resisted by stridulating strongly, raising herself on her legs and flexing the apex of her metasoma slightly towards her coxae. As soon as the male began stroking her with his antennae, she became subdued, stopped stridulating and became absolutely still. Once on the female, the male continued to flicker his antennae, continuously stroking her

head and the anterior part of her mesosoma (Fig. 3). The female remained in a frozen position, with her antennae concealed under her deflexed head. After a period ranging from several seconds to a couple of minutes, depending on her reaction, the male gradually manoeuvred posteriorly on the female so that his genitalia could be inserted into her genital opening. If she became restless the stroking of her body by his antennae intensified. If she became more restless, he would quickly resume his initial more anterior position.

After moving posteriorly, the male grasped the female laterodorsally at the midlength of the first metasomal segment with his mandibles; extruding his genitalia he began prodding her genital opening with them. Often, while the male was prodding her genital opening, the female would wander around the petri dish with him still mounted on her back. If she became too agitated or began moving too quickly, the male withdrew his genitalia, disengaged his mandibles and again began stroking her with his antennae. As soon as actual genital union occurred, the female became motionless, thrusting her body forward, tucking her forelegs under her head, with the middle and hind legs placed laterally and supporting her. Her entire body was more or less straight with the metasoma lifted and the head against the substrate. Her ovipositor was extruded (Fig. 4), a condition which may be necessary for successful copulation in mullids since it has been observed in other species (Brothers 1972, Bayliss and Brothers 1996). Genital union lasted between 60–100 seconds, during which time the male continuously stroked the female with his legs and antennae. Throughout genital union, the parameres remained outside the body of the female, lateral to her genital opening, while the rest of the male's genitalia extended into the female.

Immediately following separation of the genitalia, the male, poised posteriorly on



Figs. 3–6. *Dolichomutilla sycorax*, mating behaviour, diagrammatic. 3, mounted ♂ stroking ♀ with antennae. 4, posture immediately before copulation. 5, posture immediately after copulation. 6, posture several seconds after copulation.

the metasoma of the female, extended and straightened his metasoma, thrusting the tip high into the air, and retracted his genitalia (Fig. 5). Suddenly, without warning, the male rushed forward over the female, coming to rest on her mesosoma. He dropped his head on to hers and lifted the posterior part of his metasoma high into the air, almost perpendicular to the sub-

strate, while swaying back and forth for approximately 5–10 seconds before dismounting (Fig. 6). Immediately upon genital separation the female retracted her ovipositor and bent her metasoma forward between her legs. She bent her head down and nibbled the metasomal tip with her mouthparts. This behaviour has previously been reported as unique for the



Formicidae within the Hymenoptera (Wilson 1962, Farish 1972), but has never been recorded following copulation. Its function is not obvious but, despite the fact that no extruding material could be seen, it is possible that part of the material deposited by the male is a nuptial donation which the female consumes and uses as food or as some chemical signal. The female did not extrude and withdraw her sting as observed by Brothers (1972) in *Pseudomethoca frigida*, and by Bayliss and Brothers (1996) in *Tricholabiodes* spp. After dismounting, the male usually began grooming himself thoroughly. It was several seconds before the female began to wander around the petri dish again.

In subsequent encounters immediately following mating, the male's response to the female was one of apparent hostility; he rushed at her, fluttering his wings and bumping into her from behind. After several seconds of such treatment, and with no possible escape from the petri dish, the female stopped moving and hunched up, curling her head and antennae under her body and tucking her legs against her sides. The male continued to bump her from behind, rushing at her with wings flapping, apparently attempting to drive her away. Subsequent encounters between the male and female were of shorter duration, with continued aggressive behaviour exhibited by the male towards the female. Similarly, if two previous recently mated adults were again placed together, the male immediately became aggressive towards the female, chasing her with wings fluttering and bumping her, almost pouncing on her. The male became more aggressive to the mated female the longer they were kept together. There was never an attempt by the male to mount an already mated female. As previously observed in *P. frigida* (Brothers 1972), the attractiveness of a mated female mutillid appears to diminish rapidly after mating. After several days the aggressive behaviour

of the male towards the female had vanished, with him totally ignoring her.

Unlike the situation in some other *Smicromyrmina* (Mutillini), some *Myrmosinae* and the *Rhopalomutillinae* (Brothers 1975, 1989), where the male often transports the female in flight before settling and mating or may even mate in flight, in *D. sycorax* no attempt was made by the male to fly and carry the female, and mating took place on the substrate in an upright position. The absence of phoretic copulation is probably because the male is about the same size as the female or even smaller.

### Grooming

There are no differences in cleaning techniques between the sexes (except for those involving the wings). If an individual is extremely dirty it first partially cleans the posterior part of the body; otherwise grooming proceeds antero-posteriorly.

*Head.*—The antennae, which are the most frequently groomed structures, are cleaned using the antenna cleaners on the front legs, either by double-antenna scraping (both antenna cleaners are simultaneously passed distad along the respective ipsilateral antenna) or single-antenna scraping (one antenna at a time is groomed by the ipsilateral antenna cleaner; the different antennae are usually groomed consecutively). During double-antenna scraping, the head remains still with each antenna placed in its antenna cleaner and then drawn between the spur and basitarsus from base to apex three to four times by movement of the forelegs. During single-antenna cleaning, the leg is lifted over the antenna which is placed in and pulled through the antenna cleaner by tilting the head backwards and simultaneously moving the leg away from the head. Sometimes, more often in the female, there is simultaneous grooming of one antenna using the antenna cleaners of both ipsi- and contralateral forelegs. The

surface of the head is cleaned by both forelegs separately or simultaneously. If the head is cleaned by only one foreleg, it is tilted to one side and brushed postero-anteriorly with short rapid strokes. The brushing of the head is usually followed by single-antenna scraping. The foreleg calcaria are used for cleaning the mandibles, while both maxillary and labial palpi are cleaned similarly to double-antenna scraping, where the palpi are either singly or simultaneously pulled rapidly through the antenna cleaner of the ipsilateral forelegs. While one foreleg is cleaning the ipsilateral antenna, the other might be cleaning the palpi.

*Body.*—Cleaning of the dorsal and lateral parts of the mesosoma was never observed. The anterior part of the mesosoma, including the neck region, is cleaned with the forelegs separately or simultaneously. The mesosternum is cleaned by the calcar and basitarsus of the foreleg; the calcar is first angled away from the basitarsus, then pushed down the length of the mesosoma between the coxae, ending with the foreleg rubbing laterally against the ipsilateral middle leg. The dorsal and lateral parts of the metasoma are cleaned by both hind legs, using alternating or simultaneous strokes. While grooming the metasoma, the wasp balances on its front two pairs of legs, with the entire body slightly arched and the wings folded dorsally. Often only one side of the metasoma is cleaned, using the ipsilateral leg. The longer tibial spur, which is that mainly used, is angled away from the tibia. The metasoma is first cleaned proximally, then sequentially more distally using longer strokes each time, the first one or two segments being cleaned before proceeding to the more distal segments. The sides are groomed first, followed by the dorsal surface and then the sterna which are cleaned by a single hind leg. While the middle and hind legs clean the metasoma, the animal balances on its head with the forelegs supporting it laterally but close to the head.

Although the hind legs are predominantly responsible for cleaning the metasoma, the middle legs might assist by making several strokes down the sides. No concentration of attention to grooming of the felt lines (laterally on the second metasomal tergum) or the metasomal apex was observed, although these areas may be sources of pheromones or other chemicals.

*Legs.*—The legs are cleaned sequentially, anterior to posterior. The fore legs, if very dirty are first rubbed against each other. The entire foreleg is then rubbed against and pulled between the spur and basitarsus of the ipsilateral middle leg. The ipsilateral middle leg is not moved. Alternatively, the fore leg is positioned ventrally along the length of the body, and the spur and basitarsus of the ipsilateral middle leg is scraped down its entire length and then shaken. Cleaning of the forelegs, in particular the tarsi and apical portions of the tibiae, using the mouthparts (otherwise known as foreleg nibbling) was never observed, although Basibuyuk and Quicke (1999) noted this as commonly occurring in Mutillidae. The middle legs are groomed separately, using the tibial spurs and basitarsi of both hind legs. The hind legs are individually cleaned by the spurs and basitarsi of the ipsilateral middle and contralateral hind legs. The hind leg remains still. A hind leg is first cleaned distally, then sequentially more proximally by cleaning a longer section each time that the other legs are rubbed against it. The hind leg used for cleaning, if very dirty, is shaken or the basitarsi of both hind legs are rubbed together.

*Wings.*—The left and right wings, like the antennae, are cleaned either separately or simultaneously, using the spur and basitarsus of the ipsilateral hind leg. This is not to be confused with ichneumonid-type wing grooming where both pairs of raised wings are groomed simultaneously between the tibia and tarsus of each respective ipsilateral hind leg (Behaviour 16

(Basibuyuk and Quicke 1999)). Unlike ichneumonid-type wing grooming, where the wings are cleaned while in a horizontal position (Basibuyuk and Quicke 1999), in *D. sycorax* the wings are orientated ventrolaterally to the metasoma. While the forewings are cleaned, the hind wings are positioned laterally, perpendicular to the body and horizontal to the substrate. The wing, while being cleaned, always remains between the body and the hind leg. While the dorsal surface of the forewing is being cleaned, the costal margin is orientated ventrally with the dorsal surface facing outwards. The metatibia and metabasitarsus, remaining lateral to the wing, slowly comb it in a backward-downward motion. After 3–4 strokes the hind leg is cleaned. The posterior margin of the forewing is cleaned once the dorsal surface has been combed; it is gripped and pulled between the spur and basitarsus. Thereafter the forewing is orientated so that the costal margin is dorsally placed, with the ventral surface facing outward. The ventral surface of the forewing is cleaned similarly to the dorsal surface. The hind wing is cleaned in a sequence similar to the forewing. The latter returns to a horizontal position along the body after scraping, though at a greater distance from the body than in the normal resting position. The hind wings are similarly flipped as the forewings, depending on the surface being cleaned. When the wings of both sides are being cleaned simultaneously, the animal balances on its front and middle legs, and when cleaning the wings separately, the wasp shifts its weight to either the left or right legs, arching the mesosoma away and the metasoma towards the wing that is being cleaned.

Compared with *Tricholabiodes* spp. (Bayliss and Brothers 1996), *D. sycorax* displays relatively few differences in grooming techniques but does tend to exhibit a greater repertoire of grooming behaviours.

## Host Relations

Specimens of *Dolichomutilla* have been reared from the mud nests of various host wasps (specially sphecids of the tribe Sceliphriini) and appear to be restricted to such hosts. Nonveiller (1996) gave the host of *D. guineensis* (Fabricius) (= *D. simillima* Bischoff) as an unidentified species of *Chalybion*, and that of *D. scutellifera* (André) (= *D. conigera* (André)) as an unidentified species of *Sceliphron*. Krombein & Walkley (1962) recorded *D. minor minor* Bischoff as a parasitoid of *Sceliphron spirifex*; we have seen a female specimen of *D. m. minor* collected on a *Sceliphron* nest at Mkuzi Game Reserve, KwaZulu-Natal (27°37'S, 32°14'E) on 3–6.iii.1990 by A. Weaving (DJB collection) and a female of *D. m. minor* reared from a mud nest of "*Cyphononyx antennatus* (Smith)" (Pompilidae) collected at Durban on 10.i.1945 by Marley (South African Museum collection). Weaving (1994a, 1994b, 1995) recorded the hosts of *D. heterodonta* Bischoff in KwaZulu-Natal as *Auplopus femoralis* (Arnold) (Pompilidae), *Tricarinodynerus guerinii* (Saussure) and *Afreumenes aethiopicus* (Saussure) (both Vespidae, Eumeninae), all species using mud in nest making. (The mutillid was probably misidentified, however, since that species only occurs further north.)

Péringuey (1898) reared both sexes of *D. sycorax* from the mud nests of *S. spirifex* on several occasions. Skaife (1953:325) referred to "*D. guineensis*" (actually *D. sycorax*) as having been reared from *S. spirifex*, but gave no authority for this, and may have been referring to Péringuey's specimens. (Incidentally, Skaife's figure 163, captioned as being of both sexes of *D. guineensis* "Parasitic on solitary bees" (sic), shows a male which looks like a species of *Stenomutilla* and a female which is probably a species of *Dasylabroides*.) Weaving (1994b, 1995) recorded *S. spirifex*, *T. guerinii* and *Synagris analis* Saussure (Vespidae, Eumeninae) as hosts of *D. sycorax*,



and provided considerable information on the biologies of the hosts and the influence of nest type and construction on parasitism rates. In the Albany Museum (Grahamstown) there are three female and three male specimens of *D. sycorax* reared from a nest of *S. spirifex* which also yielded one female and one male of the host and was collected by N.J. Myers at the Tobacco Research Station, Trelawney, Zimbabwe, January/February 1954 (dets F.W. Gess). In addition to these records and the same host relationship recorded in this paper, *D. sycorax* has also been reared from multicellular mud nests of a species of eumenine vespid, possibly *Delta maxillosa* (de Geer) (det. C.F. Jacot-Guillarmod) or *S. analis* (see Weaving 1995), collected by DJB at Lake Sibaya, KwaZulu-Natal on 13–25 March 1968. That nest yielded no host specimens, but produced six mutillids, five females (10–18 mm long) and one male (10 mm long). The considerable difference in sizes of individuals in this clutch is notable. The largest female has golden brown pubescence replacing the black pubescence of the other specimens and thus appears very different in coloration. (Bischoff (1920) described a similar female specimen of this species as form *aurata*, and this phenomenon was first noted by André (1899:35) for other mutillids.) The host range of *D. sycorax* is thus greater than previously thought, although in all cases mud is used for nest construction, whether as free multicellular aerial nests or forming the nest closures and cell partitions in cavity nests.

Also interesting is the fact that for two of the three nests from which multiple mutillids emerged, a single male was produced. This may indicate a tendency toward a biased sex ratio as is found in some other parasitoid hymenopterons, specially those which develop gregariously or quasi-gregariously, and which produce a single male that emerges early and mates with his sisters as they emerge (e.g. see Hardy 1994). Additional evidence is

obviously needed, but partial support may be derived from the observation that males of *Dolichomutilla* are very much rarer in collections than are females.

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